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ECOLOGICAL ASPECTS OF ARETHUSA BULBOSA, CALOPOGON TUBEROSUS, AND POGONIA OPHIOGLOSSOIDES (ORCHIDACEAE) IN EASTERN NEWFOUNDLAND. I. FLOWERING AND FRUITING PATTERNS J. TODD BOLAND AND PETER J. SCOTT

ABSTRACT

Differences in reproductive ecology and floral characteristics were investigated in three sympatric species of peatland orchids. *Arethusa* produced the highest percentage of flowers but the lowest percentage of seed capsules while *Pogonia* showed the opposite pattern. *Calopogon* had an intermediate percentage of flowers and a low capsule set. The pollination biology of these three species is discussed.

Key Words: peatland orchids, Arethusa, Calopogon, Pogonia, floral biology, eastern Newfoundland

INTRODUCTION

Peatlands are a significant feature of Newfoundland and 18 of

the 32 species (Scott, 1981) of native orchids are inhabitants of peatland environments (Pollett and Wells, 1980). Arethusa bulbosa L., Calopogon tuberosus (L.) BSP, and Pogonia ophioglossoides (L.) Ker were chosen for this study because they are sympatric and it is common to find all three species occurring on the same bog (Luer, 1975). The flowers of these species are specifically adapted for pollination by Bombus and in Newfoundland, these orchids may be visited by either Bombus borealis Kirby or B. sandersoni Franklin. Arethusa is pollinated by queen bees, Calopogon by workers, and Pogonia by both. These species have flowers of similar size and color with yellow-white brushes on their lips which strongly absorb ultraviolet light (Thien and Marcks, 1972). They have little or no perfume or nectar. Despite their similarities in floral characters and habitat, no hybrids have been detected in nature. Thien and Marcks (1972) determined that the major isolating mechanism is placement of pollinia on the bee's body. Due to differences in lengths of columns in the three species, Pogonia places its pollinia onto the bee's head, Arethusa onto the bee's thorax, and Calopogon onto the bee's abdomen. Since stigma location is directly below the anther on the column, placement

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of pollinia onto the bee will be in the area specific to being picked up by the stigma when the bee visits the next conspecific flower. The study site chosen has a harsh climate in that cold, wet weather can occur at time of flowering. This study was undertaken to collect data for comparison with data from other parts of the species' ranges.

METHODS AND MATERIALS

Field work was conducted Jun.–Sept. 1988. Study sites were three peatland areas located about 40 km west of St. John's, Newfoundland in the vicinity of the Witless Bay Line (Site 1: elev. 216 m, 47°22′00″N, 53°02′51″W; site 2: elev. 231 m, 47°20′35″N, 52°59′14″W; and site 3: elev. 197 m, 47°20′19″N, 52°55′52″W). Site 1 and 3 are slope bogs while site 2 is a ribbed fen (classification according to Wells, 1981).

A 10 m² plot was delineated at each site and each plot was subdivided into 400.5 m² quadrats. The number of Arethusa, Calopogon, and Pogonia plants was counted in each quadrat. The total number of flowers and seed capsules was also determined for each plot. When available, the floral characters of inflorescence height from substrate surface to the base of the pedicel, natural spread of the flower, length and width of the lip, and length of the column were determined for ten flowers each of Arethusa and Pogonia from each of the three plots. The flowers of Calopogon were similarly measured, but since these orchids have a multiflowered inflorescence, the lowest flower on each of ten spikes was measured. Percent flowering of each species was determined from the ratio of flowering plants to the total plants of that species in each plot. Percent capsule set was determined from the ratio of capsules to total flowers produced by a species. Data were tested for normality using the procedure outlined in the Minitab Reference Manual (1988). Homogeneity of variance was determined using the F-test. The mean size of various floral characters was compared between sites using a pooled t-test. Statistical significance is taken to be at the 5% level.

RESULTS

The total number of plants, flowers, and seed capsules of each of the three orchid species in the 10 m² plots at each of the three sites is summarized in Table 1.

Site No.

Plants Plants with blo Seed capsules

% Flowering

% Capsules/flc

Arethusa			Calopogon			Pogonia		
1	2	3	1	2	3	1	2	3
187	25	78	33	87	155	201	921	136
	5	26	6	9	17	7	21	6
7	1	4	1	2	3	2	6	2
28.9	20.0	33.3	18.2	10.3	11.0	3.5	2.3	4.4
13.0	20.0	15.4	16.7	22.2	17.6	28.6	28.6	33.3
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Table 1. Summary of the total number of plants, flowers and seed capsules of Arethusa, Calopogon a

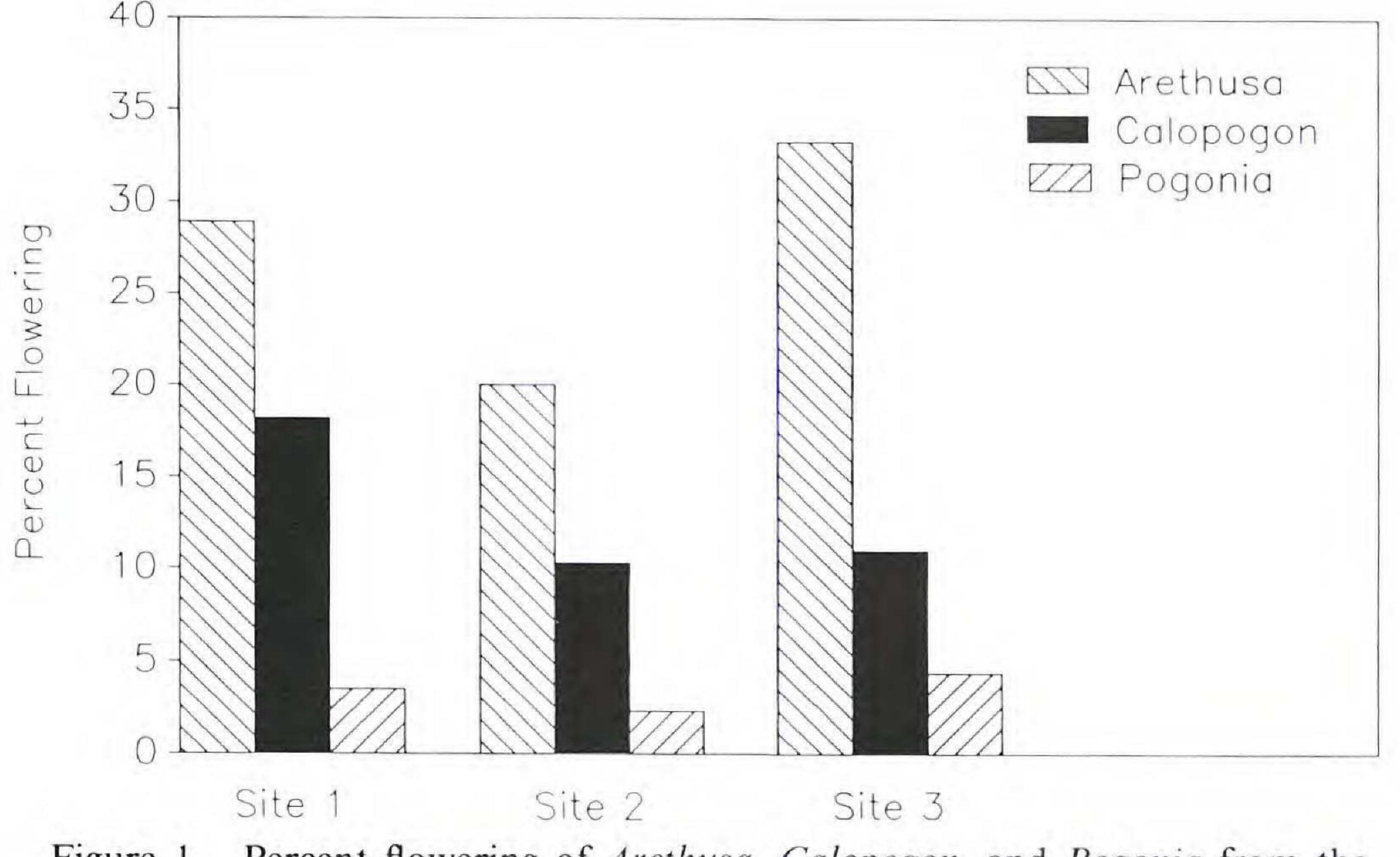
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Figure 1. Percent flowering of Arethusa, Calopogon, and Pogonia from the three eastern Newfoundland sites.

The mean percent flower production for *Arethusa* was 27.4% (range = 20.0-33.3%), *Calopogon* 13.2% (range = 10.3-18.2%), and *Pogonia* 3.4% (range = 2.3-4.4%). The mean percent capsule

set for those plants that flowered was: *Arethusa* 16.1% (range = 13.0-20.0%), *Calopogon* 18.8% (range = 16.7-22.2%), and *Po-gonia* 30.2% (range = 28.6-33.3%). Figures 1 and 2 compare the percent flowering and capsule set by the three orchids.

Measurements of the various floral characters of the three species in Newfoundland were subjected to statistical analyses and were found to be comparable to those documented from the rest of North America (Correll, 1950; Thien and Marcks, 1972; Luer, 1975), except for inflorescence height, which in Newfoundland was at the lower end of the range of values.

DISCUSSION

Arethusa had the highest percentage of plants producing flowers

with a mean of 27.4%, *Calopogon* had 13.2%, and *Pogonia* 3.4%. These values do not necessarily reflect typical flowering rates. The total number of flowers produced by these three species is quite variable from year to year. Firmage and Cole (1988) conducted a seven-year study on *Calopogon* in Maine. They found the total number of flowering plants on a single bog to vary from 101 to

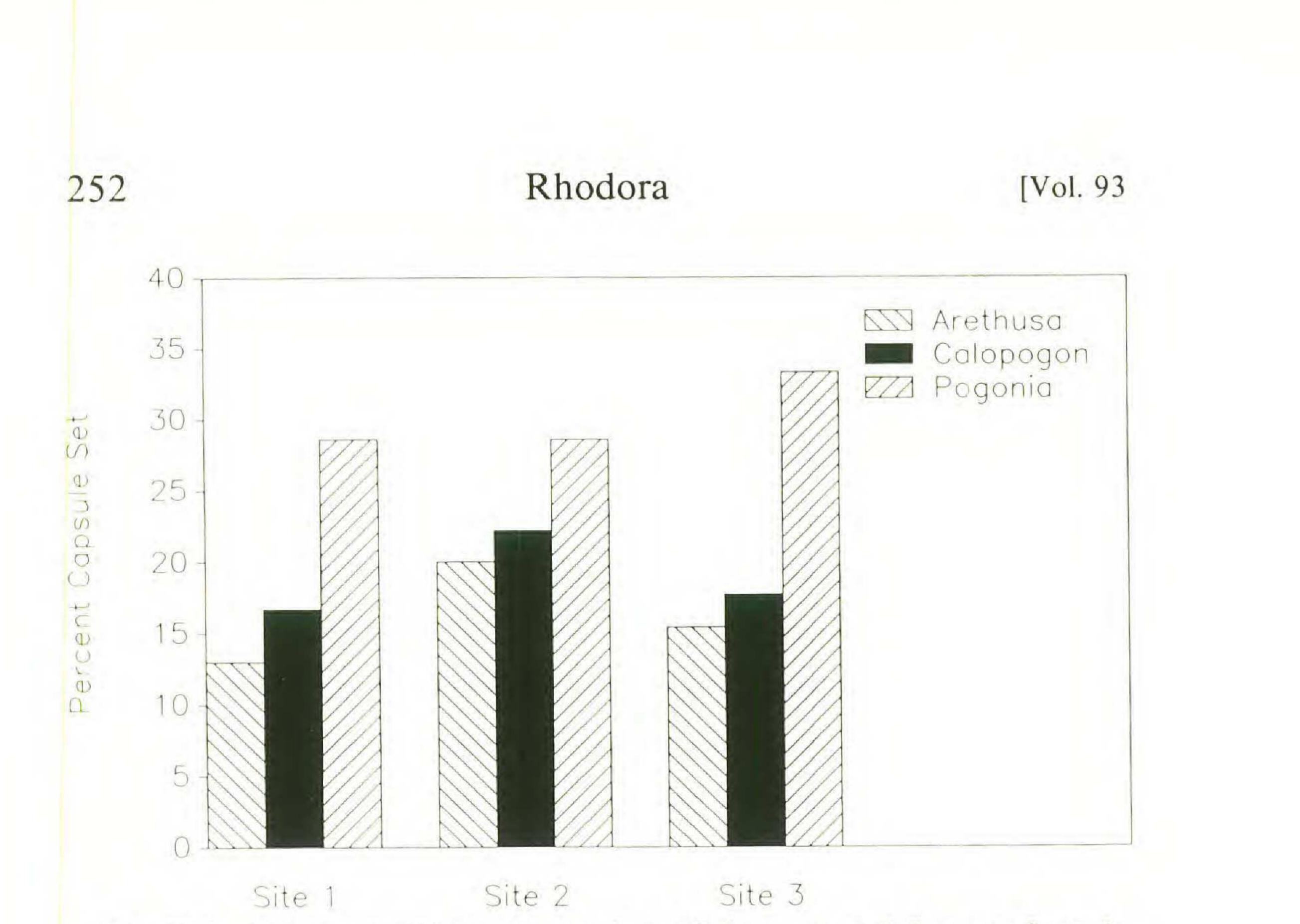


Figure 2. Percent capsule set by Arethusa, Calopogon, and Pogonia from the three eastern Newfoundland sites.

402. Case (1983) observed Arethusa on a particular bog for more than 30 years and found the number of blooming plants to fluctuate greatly. Case (1964) also noted that Pogonia may bloom abundantly in a particular bog one year but produce few flowers the next. The mean percent capsule set was lowest for Arethusa (16.1%), a little higher for Calopogon (18.8%), and highest for Pogonia (30.1%). This pattern is opposite to the mean percent flower production. Thien and Marcks (1972) studied the same three species and, as in this study, found Arethusa to have the lowest percent capsule set (5%) among the three species. Firmage and Cole (1988) found Calopogon to have a range of 12-40% capsule set over a seven year period. Thien and Marcks (1972) found Pogonia capsule set to range from 10-100%. Some populations of Pogonia appear to be apomictic, hence the 100% capsule set (Thien and Marcks, 1972). Arethusa may have the lowest capsule set due to its time of anthesis (Case, 1983). Arethusa flowers earliest, in mid-

to late June; Calopogon and Pogonia flower in July.

Despite these patterns, numbers of capsules produced by each of the three species are comparable. Among the three sites, *Arethusa* produced twelve capsules, *Calopogon* six, and *Pogonia* ten. Each species produces seed capsules of similar size (Luer, 1975), thus they should produce comparable numbers of seeds

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and have similar reproductive output. Pogonia produced fewer flowers than Arethusa or Calopogon yet was able to maintain its reproductive output at levels close to those of the other two species. Flowering is energetically expensive to a plant (Schwage, 1971). Pogonia can maintain its reproductive output with a minimal number of flowers and hence with a proportionately minimal expenditure of energy.

Overall, the number of seed capsules produced in these three

orchids is quite low compared to other non-orchidaceous bog plants. Low capsule set is the norm for many northern species of orchids (Thien and Utech, 1960). The study species are pollinated by deceit, appearing to offer food while, in fact, offering little or none (Thien and Marcks, 1972). After visiting several flowers of a nectarless plant, a bee soon learns to identify and avoid these flowers; few visits by bees result in low pollination rates. Calopogon has several ways to reduce its chances of being quickly identified by the bees. This orchid is unscented; scent is used for close-range orientation, thus the bees are forced to rely on color to identify the flower (Thien and Marcks, 1972). This orchid, as well as the other two, has flowers which are randomly variable in color, from pale pink to deep magenta. Color variability may

cause problems for the bees; after learning to avoid one shade of a species they then encounter other shades of that species (Heinrich, 1979).

Ability of bees to recognize a food source is especially problematic for low nectar-producing or nectarless plants which produce large numbers of flowers. Arethusa was in such a situation by producing the highest percentage of flowers of the three species. A concentration of low-nectar flowers in a small area allows potential pollinators to more quickly identify the flowers as nonrewarding; thus in future foraging, the pollinator will avoid those flowers. This avoidance may be another reason for the low percentage capsule set for Arethusa. Because Pogonia produced the fewest flowers, bees may not as quickly identify its flowers as being a poor food source.

Firmage and Cole (1988) suggested that Calopogon is pollinated by what Stoutamire (1967) called "chance pollination." The relatively large flowers with the ultraviolet pattern produced by pseudoanthers are attractive to bees. However, once visiting several flowers and finding no food reward, bees will avoid this species; any pollination which occurs during foraging is simply due to

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chance. The idea of "chance pollination" has been suggested by Melampy and Hayworth (1980) for *Isopyrum biternatum* L. (Ranunculaceae) and by Dafni (1983) for *Orchis caspia* Trautv. These species also lack food and are pollinated by deceit. If "chance pollination" occurs for *Calopogon*, it may equally apply to *Arethusa* and *Pogonia* since they too are pollinated by deceit.

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